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Abstract: Urbanization alters species richness and composition, but studies of urbanization effects on ecological functions have often quantified variation in functional traits and changes in functional diversity rather than measuring directly how ecological functions vary between rural and urban assemblages. Consuming dead animal matter and recycling its nutrients stabilizes and structures food webs and therefore represents a key component of ecosystem functioning. Introduction of free-ranging domestic pet animals adds additional scavenger species to urban habitats, and increased predictability of carcass resources produced by human activities characterizes urban habitats. Here, we investigate the effect of urbanization on the composition of diurnal and nocturnal scavenger assemblages and on the ecological function of carcass removal by using a carcass placement experiment in Swiss urban and adjacent rural habitats. While diurnal and nocturnal scavenger assemblages changed considerably from rural to urban areas by comprising particularly more domestic cats in the latter, carrion consumption rate did not differ between the two habitats. Predictability of carcass occurrence increased carrion consumption rate in both urban and rural habitats but mainly native scavengers and not introduced domestic pets responded to the repeated placements. These results suggest that urbanization shapes scavenger assemblage compositions without affecting their ecological function. The mechanism is likely due to a behavioural change of native scavengers in response to the occurrence of domestic pets resulting in functional plasticity of urban scavenger assemblages. The functional plasticity might be facilitated by the increased carcass predictability and additional anthropogenic food resources in urban habitats exploited by nutritionally flexible native scavenger species.

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Carcass predictability but not domestic pet introduction affects functional response of scavenger assemblage in urbanised habitats

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Abstract

1. Urbanisation alters species richness and composition, but studies of urbanisation effects on ecological functions have often quantified variation in functional traits and changes in functional diversity rather than measuring directly how ecological functions vary between rural and urban assemblages.
2. Consuming dead animal matter and recycling its nutrients stabilizes and structures food webs and therefore represents a key component of ecosystem functioning. Introduction of free-ranging domestic pet animals adds additional scavenger species to urban habitats, and increased predictability of carcass resources produced by human activities characterizes urban habitats.
3. Here, we investigate the effect of urbanisation on the composition of diurnal and nocturnal scavenger assemblages and on the ecological function of carcass removal by using a carcass placement experiment in Swiss urban and adjacent rural habitats.
4. While diurnal and nocturnal scavenger assemblages changed considerably from rural to urban areas by comprising particularly more domestic cats in the latter, carrion consumption rate did not differ between the two habitats. Predictability of carcass occurrence increased carrion consumption rate in both, urban and rural habitats but mainly native scavengers and not introduced domestic pets responded to the repeated placements.
5. These results suggest that urbanisation shapes scavenger assemblage compositions without affecting their ecological function. The mechanism is likely due to a behavioural change of native scavengers in response to the occurrence of domestic pets resulting in functional plasticity of urban scavenger assemblages. The functional plasticity might be facilitated by the increased carcass predictability and additional anthropogenic food resources in urban habitats exploited by nutritionally flexible native scavenger species.

27

28 **Keywords:** carrion, domestic cat, ecosystem services, ecological functioning, functional
29 equivalency, urbanisation

30

Introduction

Although there are numerous studies showing that urbanisation causes a decrease in species richness and diversity and changes the assemblage compositions (Marzluff 2001; Clark & Reed 2007; Grimm *et al.* 2008; Reis, López-Iborra & Pinheiro 2012; Sol *et al.* 2014; Marzluff 2017), we still have limited knowledge about how responses in assemblage composition to urban development affect ecological functions and associated ecosystem services. Changes in assemblage composition are shown to affect ecosystem functioning through the replacement of species that fulfil specific functions (Hooper *et al.* 2005; Tilman, Isbell & Cowles 2014). However, studies of urbanisation effects on ecological functions have often quantified variation in functional traits and changes in functional diversity (Schütz & Schulze 2015; Oliveira Hagen *et al.* 2017), rather than measuring directly how ecological functions vary between rural and urban assemblages.

One characteristic feature of many urban areas in the world is that free-ranging domestic pet animals, in particular domestic cats, are introduced, and they reach high population densities larger than 100 individuals / km^2 in many suburbs, outer quarters and agglomeration of cities in the western world (Lepczyk, Mertig & Liu 2004; Baker *et al.* 2008; Sims *et al.* 2008). Recent studies investigating the effects of introduced species on ecological functions revealed mainly negative effects on ecological processes, often due to competition with or direct predation on native species (Towns, Atkinson & Daugherty 2006; Tumolo & Flinn 2017). In this context, domestic cats were identified to prey on considerable amounts of urban rodents and birds (WOODS, McDonalds & Harris 2003; Lepczyk *et al.* 2004; Baker *et al.* 2005; Baker *et al.* 2008; Tschanz *et al.* 2011; Loss, Will & Marra 2013) and thus are likely to alter predator-prey interactions and trophic cascades within urbanised areas. However, until now it remains an overlooked fact that introduction of domestic pet animals also introduces facultative scavengers to urban habitats affecting carrion decomposition. Introduction of facultative scavengers might be an important general phenomenon since a high proportion of

57 the animals on the Worst Invasive Species list are facultative scavengers (Lowe *et al.* 2000;
58 Wilson & Wolkovich 2011). However, introduced facultative scavenger species may not
59 cause a decline in carrion decomposition rates: they can also replace or augment the
60 ecological function of native species (Didham *et al.* 2005; Schlaepfer, Sax & Olden 2011;
61 Bingham *et al.* 2018).

62 Consuming dead animal matter and recycling its nutrients stabilizes and structures
63 food webs and therefore represents an underestimated key component of ecosystem
64 functioning (Wilson & Wolkovich 2011; Barton *et al.* 2013; DeVault *et al.* 2016). In
65 anthropogenic ecosystems, the main consumers of carcasses providing this basic ecosystem
66 service are not obligate, but facultative scavengers (DeVault, Rhodes & Shivik 2003; DeVault
67 *et al.* 2011; Brown *et al.* 2015). Although it is critical for understanding the effect of
68 urbanisation on ecosystem functioning and services (Olson *et al.* 2012; Barton *et al.* 2013),
69 the differences between urban and rural habitats in carrion decomposition rates and the
70 habitat-dependent overlap of carrion consumption amongst scavenger species remain
71 unresolved.

72 Carcasses are not always an unpredictable food resource occurring randomly
73 distributed across landscapes, because mortality shows high spatial variation depending on
74 spatial distribution of casualty risks. In particular, human activities and anthropogenic
75 installations such as roads (road kills: e.g. Guinard, Julliard & Barbraud 2012; Bishop &
76 Brogan 2013), railways (train kills: e.g. Cserkéz & Farkas 2015), glass panels/windows (e.g.
77 Machtans, Wedeles & Bayne 2013), and power lines (e.g. Rioux, Savard & Gerick 2013)
78 accumulate unprecedented amounts of carcasses in their proximity due to casualties. Thus,
79 urban environments with a high density of hazardous installations and human activity show
80 increased predictability in carcass availabilities at specific sites. Regular occurrence of
81 carcasses at the same locations, i.e. a predictable food resource, considerably alters the cost /
82 benefit ratio of searching for carcasses (e.g. Gomo *et al.* 2017). Therefore, facultative

83 scavengers are expected to evolve behavioural strategies to identify predictable carcass
84 habitats efficiently by re-visiting locations of successful carcass discovery and by using
85 personal and social information of conspecifics and heterospecifics (Cama *et al.* 2012;
86 Newsome *et al.* 2015). Though behavioural changes are known, it remains unclear how
87 increased predictability of carcass availability shapes vertebrate scavenger assemblage and
88 ecosystem processes in urbanized areas.
89 Here, we investigate the temporally separated diurnal and nocturnal scavenger
90 assemblages in Swiss anthropogenic landscapes by using a carcass placement experiment
91 monitored by camera traps. While controlling for site-specific characteristics affecting the
92 visual and olfactory abilities of scavengers such as vegetation height or weather conditions
93 (DeVault & Rhodes 2002; Selva *et al.* 2005) and thus the detection of carcasses, we focused
94 on the differences in assemblage composition and carrion consumption between urban and
95 adjacent rural habitats. Due to the increase in the total number of scavenger individuals, we
96 expect that the high density of domestic pet animals in urban habitats augments the ecological
97 function of "carcass removal" of native facultative scavengers and thus, carrion
98 decomposition rate should be higher in urban than in rural areas. In a second step, we
99 increased predictability of experimental carcass placement in both habitats to study the effect
100 of predictability on the carrion consumption of the different assemblages. The study allows an
101 enhanced understanding of privately owned domestic pet introduction and predictability of
102 food resources and thus, gives insights into the effect of urbanisation on the ecological
103 function of carrion decomposition.
104
105 **Material and Methods**
106 **Study area and experimental design**
107 The study area was located in the canton of Fribourg in Switzerland at 600 – 900 m.a.s.l. and
108 covered an area of 281.5 km^2 (Figure S1, Supporting Information). The landscape is mostly

109 dominated by agricultural fields but is considerably populated in villages and small cities.
110 Building density over the whole study area was 59 buildings per km^2. In Switzerland, there
111 are roughly 1.4 million domestic pet cats (1 million of them free-ranging), resulting in one cat
112 in more than every fourth household, with emphasis in urban areas and settlements (Turner
113 2000). In Zürich, a city in 140 km distance, around 430 domestic pet cats and 15 red foxes
114 occur per km^2 (Kistler, Gloor & Tschanz 2013).

115 Carrion consumption and scavenger assemblages were investigated by carcass
116 placement experiments from July to September 2016 (65 field days). Single vole or mouse
117 carcasses were placed and monitored by wildlife camera traps (Reconyx HC500 HyperFire™;
118 RECONYX Inc., Holmen WI, USA). The picture resolution of the camera traps was set to
119 1920 x 1080 px, the night mode was set to high quality and the "Passive Infrared Motion"
120 sensitivity to high. There was no quiet period between two trigger events (set to zero) and the
121 number of pictures per trigger was set to ten. Camera traps were installed three days before
122 placing carcasses (at least two full days with camera traps without carcasses) to prevent
123 cameras from being a cue for food. The camera traps were fixed 50 cm above ground at
124 inconspicuous plastic posts.

125 The carcasses were placed on the ground at two metres distance to the camera traps.
126 For carcass placement, small carcasses that can be removed and consumed by one scavenger
127 individual were chosen. We used wild vole and mouse carcasses from agricultural pest control
128 killed by mouse traps (European water voles, *Arvicola terrestris*, and common voles,
129 *Microtus arvalis*), because carcasses of breeding animals such as day-old chickens are
130 removed at a lower rate (Prosser et al. 2008). The rodents were frozen at the day of catching
131 and defrosted again in the fridge the day before placement. On average the carcasses weighted
132 56 g (mean weight ± sd = 56.4 ± 31.4 g, range: 10.6 g - 183.5 g, n = 716) and had a size of 12
133 cm (mean body length of rodents without tail ± sd = 12.1 ± 2.6 cm, range: 6.0 cm - 23.0 cm, n

= 716; for more details see Table S1, Supporting Information). In total a biomass of 40.4 kg carcasses was placed.

At the large spatial scale, we selected the sites of carcass placement by producing an urban and a rural habitat layer of the study area based on the Swiss digital map (vector25 © swisstopo; DV002232.1). The urban habitat layer consisted of the building and settlement structure layer including a 50 m buffer on all polygon features, but excluding forest patches and a buffer of 50 m from the forest edge to avoid the potential effects of forests. The rural habitat layer consisted of all areas outside the buffered settlements and forests. 126 locations in each of the two habitat layers (urban, rural; total: 252 locations) were randomly selected, one-third of them (42 locations per habitat category) within 30 m from roads (tarred roads with minimal 1.8 m width). At the local scale, sites of carcass placement were moved using the following rules to minimally standardize the sites and minimize variation due to local habitat differences: carcasses were placed at least four meters from houses and trees, at least two meters from hedges and, on fields or meadows, at least two meters from the edge. In each habitat category, three categories of vegetation height were randomly chosen (0 cm, 5 – 10 cm, and 20 – 25 cm). Thereby the random locations represented starting points where the search for the nearest location with the right category of vegetation height started. The carcass placement site selection procedure resulted in clear differences between urban and rural sites in the number of buildings in a 50 m radius (urban: mean ± SD = 4.08 ± 3.12 buildings; rural: 0.04 ± 0.2 buildings), in a 100 m radius (urban: 11.41 ± 8.24 buildings; rural: 0.50 ± 1.03 buildings), in the proportion of land covered by impervious surfaces in a 50 m radius (urban: mean ± SD = 42 ± 23 %; rural: 6 ± 4 %), and in a 100 m radius (urban: mean ± SD = 35 ± 19 %; rural: 6 ± 3 %). The carcass placement sites showed no spatial autocorrelation (see Supporting Information Figure S2).

Carcasses were placed after dawn (between 06:00 and 09:00 am) and again at the same location before dusk (between 05:00 and 08:00 pm). If the carcass placed at dawn was

still there, it was replaced at dusk. Thus, at each location a fresh carcass was provided first to diurnal scavengers and then to nocturnal scavengers (two carcasses per location). At 27 locations, we continued carcass placements at dawn and dusk for the subsequent four days and nights to investigate changes in the consumption rate and scavenger assemblage composition if carcass occurrence became predictable in space. This resulted in a total of five days and nights of carcass placements at the same location. In total, 720 carcasses were placed at 252 locations (Table 1). In five cases (0.7 %), data were missing due to technical failures.

Data extraction from camera trap pictures

Every carcass placement event resulted in either consumption or not. Camera pictures provided the time of carcass removal by a scavenger, enabling the calculation of the time from placement to carcass removal. In cases where placement was not clearly at day or night, placement time was corrected by using the daily nautical twilight levels, so that carcass exposure for diurnal scavengers started after the nautical twilight in the morning and for nocturnal scavengers with the beginning of the nautical twilight in the evening. The scavenger species removing the carcass was determined wherever possible; otherwise it was categorised as unknown. Diurnal and nocturnal mean values (from dawn to dusk and from dusk to dawn, respectively) of hourly temperature, precipitation, and wind of the meteorological station in Posieux (canton Fribourg, Switzerland, elevation: 646 m.a.s.l.) were used (MeteoSchweiz, Zurich, Switzerland).

Statistical analyses

The statistical analyses were performed using R (version 3.3.3, R Core Team 2017). Carrion consumption was analysed using a mixed effect cox-proportional hazard model by including the time to consumption. This regression model is commonly used to investigate the

186 association between time to event (in our case the time to consumption) and predictor
187 variables, allowing for censured data where the event is not observed in all cases due to
188 restricted observation time. In the results, a hazard ratio (HR) above one indicates that, as the
189 predictor variable increases, the event hazard increases and thus the time to consumption
190 decreases. A HR equal to one indicates no effect. Thus, effects were denoted as important
191 effects if 95% CI of HR did not overlap one. To be able to include random factors the *coxme*
192 function of the *coxme* R package was used (Therneau 2015a). The model included a time
193 variable (time to carrion consumption) and a status variable (carcass consumed or not) as
194 response variables. However, since time to consumption was only available for a reduced
195 sample of the placement experiment (208 carcass removals in 602 placement experiments),
196 we also analysed the total sample (321carcass removals in 715 placement experiments) using
197 the status variable (carcass consumed or not) as response variable in a generalised linear
198 mixed model (GLMM, fit by maximum likelihood, Laplace approximation) with binomial
199 error distribution and logit-link function. A nested random factor (location nested in date) was
200 included into the model structures of both models to account for temporal and spatial
201 dependence of the carcass placements. The following fixed effects were part of the models:
202 daytime (diurnal vs. nocturnal), habitat category (urban vs. rural areas), vegetation height
203 category, repetition at the same location, carcass weight, date, distance to the next road,
204 distance to the next forest and distance to the next building as well as the three weather
205 variables temperature, precipitation and wind. The full models included all possible two-way
206 interaction terms with the temporally separated assemblages and habitat categories except the
207 interactions with weather variables. Temperature and date were included as quadratic effects.
208 All continuous explanatory variables were scaled before they entered the model. The final
209 models were selected by backward elimination of non-significant interaction and quadratic
210 effects but keeping all main effects in the models. As random factors were close to zero, cox-
211 proportional hazard models without random effects were used to produce figures (coxph

212 model function of survival R package; Therneau 2015b) as well as to conduct model
213 diagnostics. The assumption of proportional hazards in the cox model was tested and not
214 refuted by visually checking the scaled Schoenfeld residuals (ggcoxzph function of survimer
215 R package;Kassambara & Kosinski 2017) and no single observation exceptionally influenced
216 the model.
217 The factors affecting the composition of the scavenger assemblage were analysed
218 using a multinomial logistic regression model (multinom model function of nnet R package;
219 Venables & Ripley 2007). For this analysis, the scavenging events were grouped into the
220 following categories: consumed by wild mammals, domestic pets, corvids, raptors, unknown
221 scavengers or not consumed. We included these groups as response variable and the
222 assemblage category (diurnal vs. nocturnal), the habitat category (urban vs. rural), the
223 repetition counter at the same location, vegetation height and the weight of the carcass as
224 predictor variables. We calculated confidence intervals for the model estimates of the
225 scavenger groups using tidy function of R package broom (Robinson 2019) and applied a
226 likelihood-ratio test (Anova function of car R package; Fox & Weisberg 2019) to test the
227 overall effect of the explanatory variables.
228
229 **Results**
230 In 65 days and nights the wildlife camera traps took 180'172 pictures. In total 45% of the
231 carcasses were consumed (321 out of 715) within less than twelve hours. Within the first day
232 and night of carcass placements, 43% of the carcasses were consumed (213 out of 499),
233 whereas in the repetition days 50% of the carcasses were consumed (108 out of 216). In 35 %
234 of the removals (112 out of 321 removals), scavenger species could not be identified, most
235 probably because the removal happened too rapid for the triggering (0.2 s). The average time
236 to consumption for the consumed carcasses was 210.6 min (SD = 157.7 min; N = 321; for
237 group means of the time to consumption see Supporting Information Table S4). The wildlife

238 camera traps recorded ten scavenger species removing carcasses (four bird species: carrion
239 crow *Corvus corone* (22 % of 209 removals), Eurasian magpie *Pica pica* (6 %), red kite
240 *Milvus milvus* (6 %), common buzzard *Buteo buteo* (1 %), and six mammal species: red fox
241 *Vulpes vulpes* (33 %), stone marten *Martes foina* (1 %), European hedgehog *Erinaceus*
242 *europaeus* (< 1 %), European polecat *Mustela putorius* (< 1 %), domestic cat *Felis catus* (27
243 %), domestic dog *Canis familiaris* (3 %), Supporting Information Table S2).
244
245 *Urban habitats*
246 The two analyses of carrion consumption (cox proportional hazard model and GLMM)
247 showed very similar results. Thus, results of the GLMM are shown in the Supporting
248 Information (Table S3). Time to carrion consumption (and consumption rate in the GLMM)
249 tended to be higher in the night than during the day, yet the difference was not statistically
250 significant (as defined by CI not including one, Table 2). Time to consumption also showed
251 no differences between rural and urban scavenger assemblages (Table 2, Fig. 1a). In contrast
252 diurnal and nocturnal as well as rural and urban scavenger assemblages differed considerably
253 in their composition (Table 3, Fig. 1b). The nocturnal assemblage consisted mainly of
254 mammals (wild and domestic) while in the diurnal assemblage, birds (corvids and raptors)
255 and domestic pets, mainly domestic cats, were the predominant scavengers. The most
256 common scavenger in nocturnal assemblages was the red fox and in diurnal assemblages the
257 carrion crow. Raptors occurred only in diurnal scavenger assemblages and predominantly in
258 rural areas. In urban assemblages, domestic pets were considerably more important than in
259 rural assemblages during daytime and at night. They represented always around 50% of the
260 known scavengers. In diurnal assemblages, the dominance of carrion crows in rural areas
261 changed to a share with European magpies in urban areas.
262
263 *Predictability*

264 Repeated carcass placement at the same location over several days reduced the time to carrion
265 consumption in both urban and rural areas (Table 2, Fig. 2a). The cumulative carcass survival
266 after 10 hours was 0.77 (CI: 0.72 – 0.86) at the first placement and 0.46 (CI: 0.38 – 0.75) at
267 the fifth placement, a 31 % decrease after four repetitions (see also results of the GLMM in
268 the Supporting Information, Table S3). The composition of the scavenger assemblage
269 changed with increasing number of repetitions at the same location, suggesting that
270 predictability of carcass location had a larger effect on consumption rate of some scavenger
271 species than on that of others (Table 3, Fig. 2b). In diurnal scavenger assemblages, repetition
272 resulted in increasing proportions of raptors and corvids removing carcasses. In particular red
273 kites showed a strong increase. This was the case in both urban and rural assemblages. While
274 for raptors the increase was stronger in rural areas, it was stronger for corvids in urban areas.
275 In nocturnal scavenger assemblages, repetition resulted in increasing proportions of red foxes,
276 and this effect was stronger in rural than in urban areas. Moreover, consumption rate tended
277 to decline with distance from roads.
278
279 *Factors affecting carcass detectability*
280 Several factors associated with detectability of carcasses affected time to carrion consumption
281 by the scavenger assemblages: vegetation height, carcass weight and wind speed (Table 2).
282 While high vegetation resulted in longer time to carrion consumption than short vegetation,
283 large carcasses and slightly windy conditions resulted in faster carrion consumption than
284 small carcasses or conditions without wind (range of carcass weight: 10.6 g - 183.5 g range of
285 wind speed: 1.2 - 19.0 km/h). Despite the higher consumption rate of large-sized carcasses, a
286 higher proportion of red foxes consumed small carcasses, whereas corvids, raptors and
287 domestic pets showed increased consumption rates of large carcasses (Table 3).
288
289 **Discussion**

290 In this study, we present two main results associated with urbanisation of scavenger
291 assemblages. First, while scavenger assemblages changed considerably from rural to urban
292 areas by including more domestic pets in the latter, carrion consumption rate did not differ
293 between the two habitats. Second, predictability of carcass occurrence increased carrion
294 consumption rate in both urban and rural habitats but only native scavengers and not
295 introduced domestic pets responded clearly to the repeated placements. These results suggest
296 that urbanisation shapes scavenger assemblage compositions without affecting their
297 ecological function and that urbanisation slows down the response to predictability of carcass
298 occurrence.

299 As expected, the main difference of urban compared to rural scavenger assemblages
300 was the higher proportion of introduced domestic pets, in particular domestic cats, and the
301 associated lower proportion of native facultative scavengers. The results show that both
302 diurnal and nocturnal assemblages can maintain, but not augment the functional level of
303 scavenging in urban compared to rural ecosystems though domestic pets consumed about half
304 of the removed carcasses. Our findings suggest that introduction of domestic pets has a
305 neutral effect on the ecological function of carrion consumption in cities. This functional
306 equivalency, i.e. the performance of an ecological function by different assemblages at similar
307 rates (Hubbell 2005), might be the result of two possible mechanisms in our urbanisation
308 study. First, functional redundancy (Huijbers *et al.* 2015): domestic pets may replace the
309 ecological function of reduced numbers of native scavengers in settlements. However, urban
310 areas in Switzerland and other European countries show higher rather than lower densities of
311 facultative scavengers compared to rural habitats (see Gloor *et al.* 2001 for red fox; Knaus *et*
312 *al.* 2018 for carrion crow). Thus, functional replacement in urban habitats is likely not the
313 outcome of the numerical replacement of scavenger individuals. Second, domestic pet
314 depression (Bingham *et al.* 2018; Cunningham *et al.* 2018): introduced domestic pets
315 suppress the activity of native scavenger species and the reduced consumption is replaced by

316 their own scavenging. Our results support a functional replacement by a behavioural change
317 of native facultative scavengers due to the presences of the introduced species. Most
318 probably, the suppression operates not through direct interactions, as cats are unlikely to scare
319 away carrion crows or magpies, but through depletion of randomly distributed carcasses.
320 Thus, searching for small carcasses may become less profitable so that native facultative
321 scavengers switch to more profitable food resources such as anthropogenic food waste
322 (Contesse *et al.* 2004; Newsome *et al.* 2015). As a consequence, the alimentary flexibility of
323 native facultative scavengers results in a high functional plasticity of scavenger assemblages
324 in urbanised landscapes.

325 Predictability of carcass occurrence increased consumption rate in native scavenger
326 species, but not in introduced domestic pets. The strongest response to repeated placement
327 showed red foxes and red kites, while corvids responded less pronounced. This behaviour was
328 expected since predictability of carrion resources changes the cost/benefit ratio of foraging
329 strategies and has been shown to have multiple effects on space use, foraging behaviour and
330 foraging success (Deygout *et al.* 2010; Monsarrat *et al.* 2013; Sloat & Reeves 2014). In
331 addition, also the increased consumption rate in short distances to roads supports the
332 functional response to predictability since road kills represent a highly predictable carrion
333 resource. Unlike native scavengers, free-ranging domestic pet animals are provided with
334 supplemental food by their owners and scavenging may play a limited role in their food
335 acquisition. Thus, a behavioural response to predictability might give introduced domestic
336 pets only limited benefit in terms of higher food intake. Foraging strategies of domestic pets
337 seem to be constant irrespective of predictable occurrence of resources. The high proportion
338 of domestic pets in urban carrion consumption therefore seems to results in a deferred
339 functional response of urban assemblages to newly developed sites of high carcass
340 predictability. However, the results suggest that, if established, sites of high carcass

predictability are mainly used by native scavengers in rural and urban habitats, in particular by red kites in diurnal and red foxes in nocturnal assemblages.

Urbanisation also resulted in further changes: compared to diurnal rural assemblages, the proportion of raptors decreased and the dominance of carrion crow in the group of corvids was reduced in favour of European magpies in urban assemblages. While raptors seem to be outcompeted in the use of randomly distributed carcasses, at least red kites responded strongly to carcass predictability and seem to focus on the exploitation of sites of high carcass predictability. In the case of corvids, European magpies are less common in rural areas (Knaus *et al.* 2018), but share carrion consumption with carrion crows in urban habitats. However, since carrion consumption rate by corvids did not differ between urban and rural areas, we also propose a switch of carrion crow foraging strategies to other food resources than randomly distributed carcasses. While carrion crows showed a functional response to carcass predictability, European magpies did not. Together, these results suggest that in general, predictable food resources are monopolized by few larger and more competitive facultative scavenger species in urban and rural assemblages (DeVault *et al.* 2011; Inger *et al.* 2016), since predictability also increases competition (Deygout *et al.* 2010; Oro *et al.* 2013; Sloat & Reeves 2014). In contrast, smaller, less competitive species may have to focus on randomly distributed resources.

Though the assemblages' composition of ten actively scavenging species was comparable to other studies in highly modified anthropogenic landscapes of Western Europe (e.g. Inger *et al.* 2016; Henrich, Tietze & Wink 2017), consumption rate was considerably higher in our study. While Henrich *et al.* 2017 found a consumption rate of around 0.4 dead day-old chickens per 24 hours in southwestern Germany, the same rate was reached within 12 hours in our study when placing voles. Under the assumption that the type of carcass is not the main reason for the difference, this result suggests that the diurnal and nocturnal assemblage together would have consumed the double amount of carcasses day^{-1} compared to

367 the study of Henrich *et al.* 2017. This is likely due to differences in the availability of food for
368 facultative scavengers affecting their density or foraging behaviour. We suggest that a higher
369 food availability in Switzerland resulting in increased scavenger densities is more likely than
370 a lower food availability resulting in increased searching efforts because Swiss landscapes are
371 shown to provide high amounts of food (Contesse *et al.* 2004; Cereghetti *et al.* 2019). It
372 remains a topic of future research whether and how such high consumption rates affect
373 carrion decomposing microbes and arthropods, as they compete with vertebrate scavengers
374 for carcasses (DeVault *et al.* 2003; Barton *et al.* 2013).

375 In agreement with our results also other carcass placement studies showed, that
376 characteristics of the placement location and weather conditions affected the consumption rate
377 (DeVault & Rhodes 2002; DeVault, Brisbin & Rhodes 2004; Selva *et al.* 2005; Santos,
378 Carvalho & Mira 2011) and the scavenger assemblages (Schlacher *et al.* 2013; Huijbers *et al.*
379 2015; Huijbers *et al.* 2016). As vegetation height and wind clearly affected carrion
380 consumption in the present study, consumption rates were highly site- and weather-specific.
381 We therefore suggest that vegetation height and wind conditions affect the visual and the
382 olfactory abilities of avian and mammalian scavengers (DeVault & Rhodes 2002): carcasses
383 in low vegetation might be better visible and also disseminate a stronger smell. This would
384 result in higher detection probabilities by scavengers than carcasses in high vegetation.

385 Although we attempted to control for site-, weather-, date- and carcass-specific
386 differences, we have to point out a number of limitations in our experimental study. First, we
387 used as similar carcasses as possible, but as the results show, consumption rates depended on
388 carcass characteristics. Since different scavenger species might prefer different types of
389 carcasses, using other carcass types might have changed the results. Second, even though we
390 used camera traps with rapid triggering, in c. 35% of carcass removals the scavenger could
391 not be identified, most probably due to very rapid removing behaviour. In particular, the

consumption rate of red kites might be underestimated in this study because red kites often just swooped down and grasped the carcasses without landing on the ground.

In conclusion, the scavenger assemblage in European settlements and cities provides important ecosystem services. Consumption of carrion is high and reduces the exposure of humans to rotting carcasses which likely reduces the transmission of infectious diseases. Though carcass removal remains similar compared to rural areas, urbanisation seems to change the importance of randomly distributed carcasses in the diet of native facultative scavengers. However, native scavengers most likely profit from increased carcass predictability, even though this might be only true for a few species because increased competition could result in monopolisation of predictable resources. We suggest that functional plasticity in urban scavenger assemblages is facilitated by the increased predictability of carcass occurrence and the large additional anthropogenic food resources provided in urban habitats to nutritionally highly flexible native scavenger species.

Authors' contribution

NW, PS and MUG conceived the ideas and designed methodology. NW and PS collected the data. NW analysed the data. NW and MUG led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data statement

Data are deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.q83bk3jdb (Welti et al. 2019).

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1 [Summary statistics of the placed carcasses]

Table S2 [Summary of observed scavengers]

Table S3 [Factors affecting carrion consumption in 715 placement experiments]

Table S4 [Overview of time to consumption by habitat, daytime and repetition]

Figure S1 [Map of study area with placement locations]

Figure S2 [Test results investigating autocorrelation]

Appendix S1 [R code of analyses]

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Tables

Table 1. Sample sizes of carcasses placed at different locations. At each site, half of the carcasses was placed at day and at night, respectively. Repeated placements were done in the subsequent four days and nights after the first placement.

	n carcasses	n locations
Total	720	252
Placement experiments	504	252
Urban areas	252	126
Rural areas	252	126
Road proximity	168	84
Urban areas	84	42
Rural areas	84	42
Without road proximity	336	168
Urban areas	168	84
Rural areas	168	84
Repeated placement experiments	216	27
Urban areas	104	13
Rural areas	112	14
Road proximity	72	9
Urban areas	32	4
Rural areas	40	5
Without road proximity	144	18
Urban areas	72	9
Rural areas	72	9

Table 2. Model estimates of factors affecting time to carrion consumption using a mixed effects cox proportional hazard model including a nested random effect for location and date (N = 602 carcasses placed and 208 consumption events with known time to consumption). Important effects are shown in bold. A hazard ratio (HR) above one indicates that, as the predictor variable increases, the event hazard increases and thus the time to consumption decreases (negatively associated). A HR equal to one indicates no effect. 95% confidence interval of the HR is given.

Variable	Estimate	SE	HR	95% CI
Nocturnal (vs diurnal)	0.289	0.193	1.336	0.916 - 1.948
Rural (vs urban)	- 0.103	0.247	0.902	0.556 - 1.464
Repetition	**0.197**	**0.051**	**1.218**	**1.102 - 1.345**
Vegetation height	**- 0.609**	**0.094**	**0.544**	**0.452 - 0.654**
Carrion weight	**0.168**	**0.075**	**1.183**	**1.022 - 1.370**
Date	- 0.085	0.089	0.919	0.772 - 1.094
Distance to road	- 0.120	0.079	0.887	0.759 - 1.036
Distance to forest	- 0.046	0.080	0.955	0.817 - 1.118
Distance to building	0.043	0.120	1.044	0.826 - 1.321
Temperature mean	0.024	0.096	1.024	0.849 - 1.235
Precipitation mean	0.110	0.069	1.116	0.974 - 1.279
Wind mean	**0.199**	**0.074**	**1.220**	**1.055 - 1.411**

Random effects: location nested in date: sd = 0.019; date: sd = 0.004.

Table 3. Model estimates of the multinomial logistic regression model and results of the likelihood-ratio tests. Scavengers observed taking carrions were combined in groups (N = 321 consumption events out of 715 placed carcasses). Reference level: no consumption, E = estimates, CI = confidence interval**.** Important effects are shown in bold.

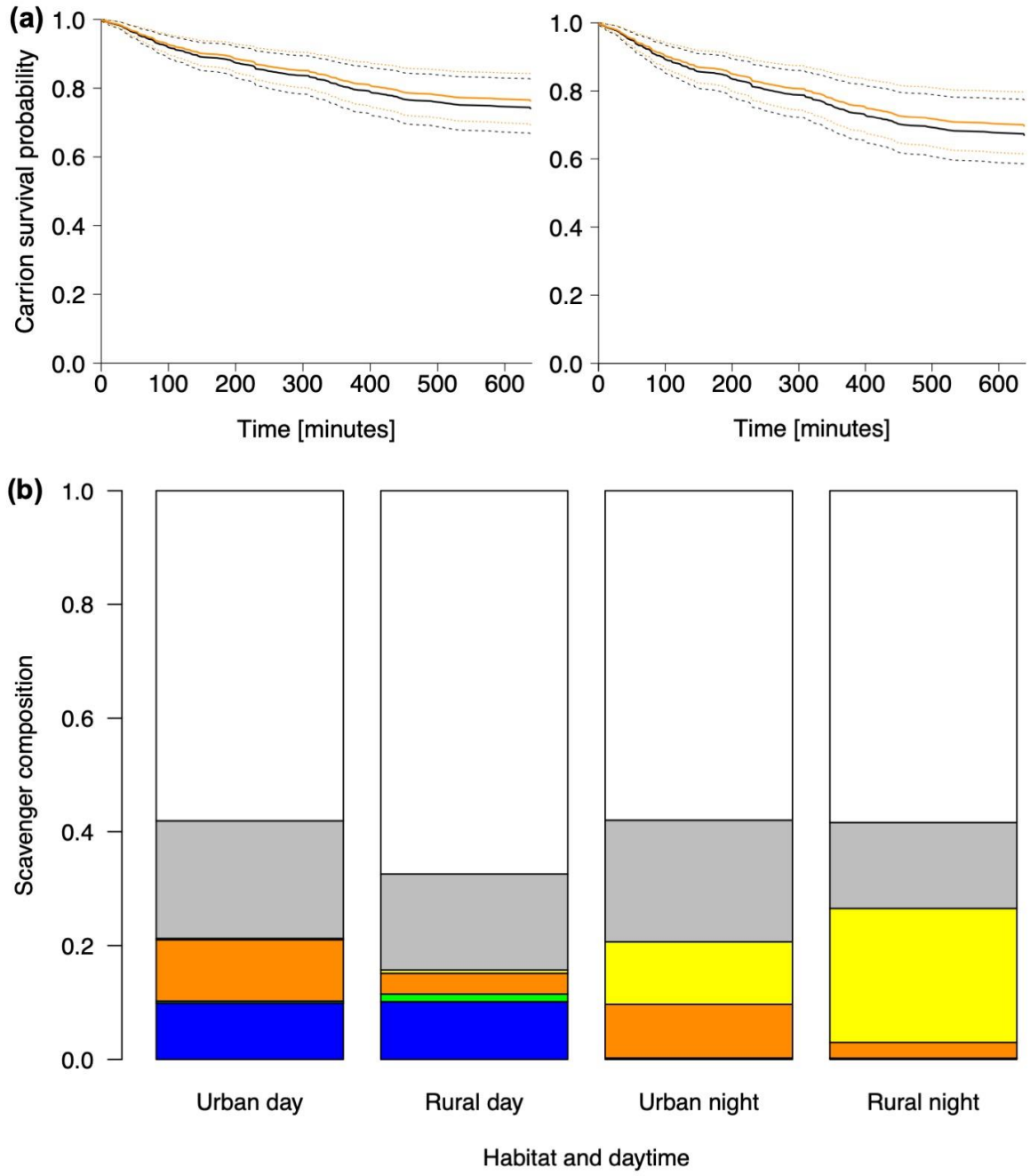
Variable	**Corvids**		**Raptors**		**Unknown scavengers**	
	E	CI	E	CI	E	CI
Intercept	**-1.97**	**-2.82 – -1.13**	**-6.24**	**-8.86 – -3.62**	**-1.02**	**-1.59 – -0.45**
Night (vs day)	**-3.65**	**-5.64 – -1.66**	**-13.0**	**-13.0 – -13.0**	0.04	-0.38 – 0.45
Rural (vs urban)	-0.13	-0.74 – 0.49	1.19	-0.40 – 2.78	-0.36	-0.78 – 0.07
Repetition	**0.21**	**0.00 – 0.42**	**0.59**	**0.21 – 0.97**	-0.04	-0.22 – 0.14
Vegetation height	**-0.08**	**-0.12 – -0.04**	**-0.09**	**-0.17 – 0.00**	-0.01	-0.04 – 0.01
Carrion weight	**0.01**	**0.00 – 0.02**	**0.02**	**0.00 – 0.05**	0.00	-0.00 – 0.01

Variable	**Domestic pet**		**Wild mammals**		**Likelihood ratio test**	
	E	CI	E	CI	LR	P-value
Intercept	**-1.56**	**-2.32 – -0.82**	**-5.02**	**-6.58 – -3.46**	--	--
Night (vs day)	-0.13	-0.71 – 0.45	**3.83**	**2.41 – 5.26**	**158.48**	**< 0.05**
Rural (vs urban)	**-1.23**	**-1.86 – -0.61**	**0.76**	**0.16 – 1.35**	**32.77**	**< 0.05**
Repetition	0.18	-0.03 – 0.38	**0.28**	**0.08 – 0.48**	**20.86**	**< 0.05**
Vegetation height	**-0.09**	**-0.13 – -0.05**	**-0.06**	**-0.09 – -0.02**	**50.45**	**< 0.05**
Carrion weight	**0.01**	**0.00 – 0.02**	-0.00	-0.01 – 0.01	**14.15**	**< 0.05**

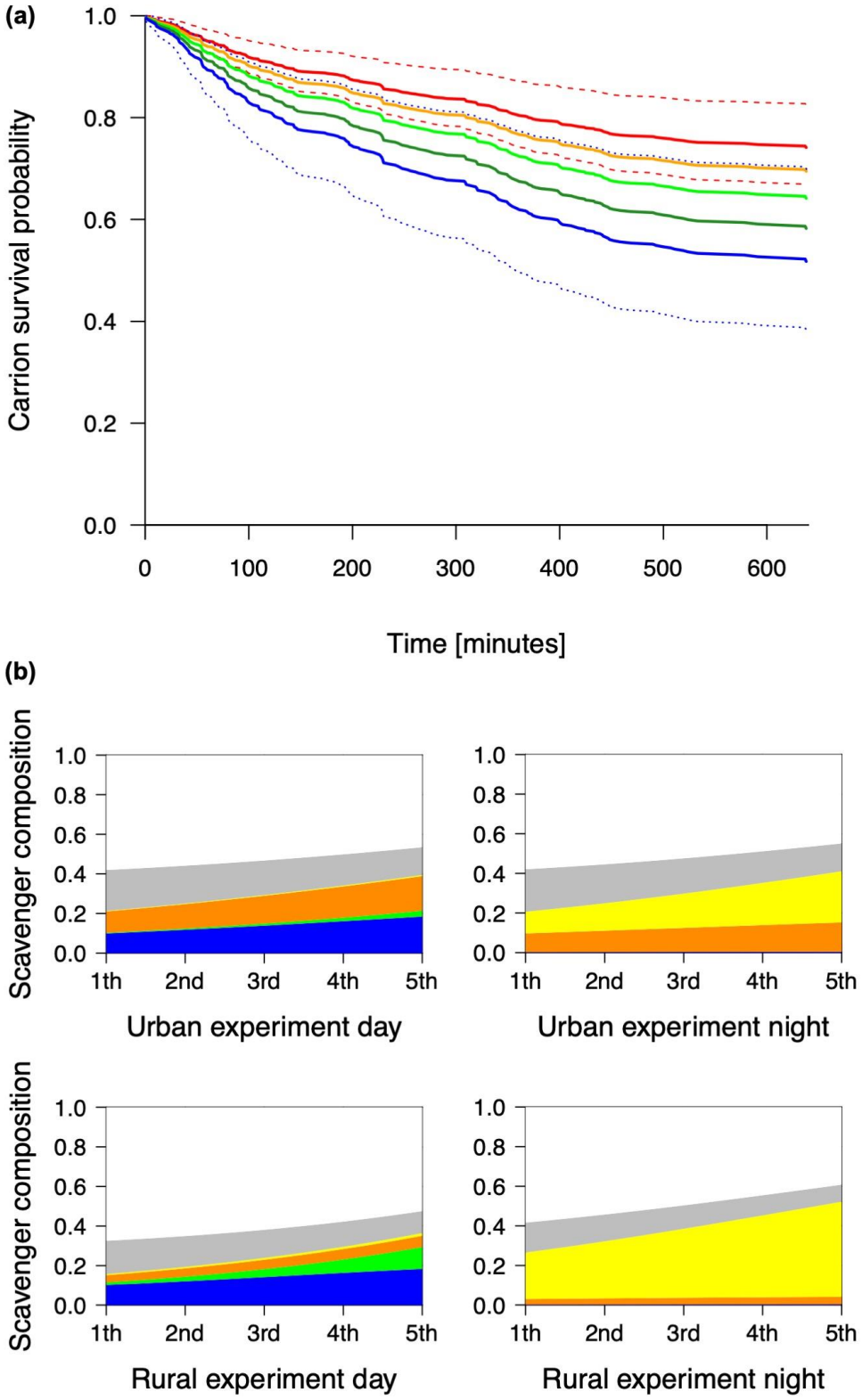
Figure legends

Fig. 1: (a) Predicted values of carcass survival probability over time in urban (black) and rural (orange) habitats for diurnal (left) and nocturnal (right) scavenger assemblages. N = 602 carcasses. Broken lines represent 95% confidence intervals. (b) Predicted scavenger composition (multinomial logistic regression model) in urban and rural assemblages during day and night. N = 321 consumption events out of 715 placed carcasses.

Fig. 2: (a) Predicted values of carcass survival probability over time for repeated placements. Values for urban habitats at subsequent repetition days are shown. N = 602 carcasses. Broken lines represent 95% confidence intervals (for the purpose of clarity only shown for the first and fifth day). (b) Predicted changes in scavenger composition over repeated placements in urban and rural assemblages during day and night. N = 321 consumption events out of 715 placed carcasses.



Welti et al. Fig. 1.



Welti et al. Fig. 2.